THE PHOTOCHEMICAL NATURE OF THE PHOTSENSORY PROCESS.

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I.

Many animals which are sensitive to light respond by an invariable, characteristic reflex. Typical of such organisms are the ascidian, Ciona intestinalis, and the common, North Atlantic, long-neck clam, Mya arenaria (Fig. 1). Both of these animals, when illuminated, respond by a vigorous retraction of the siphons. The properties of their sensitivity have been investigated to some extent, and have been described in a series of papers (Hecht, 1918–19, a, b, c, d). As a result, an hypothesis has been suggested which accounts for this type of irritability in terms of an underlying, chemical mechanism.

In its essentials this hypothesis involves the behavior of two processes: one, a reversible photochemical reaction; the other, an ordinary, simple, chemical reaction. The light acts on a photosensitive substance $S$ and decomposes it into its two precursors $P$ and $A$. The degree of sensitivity of the sense organ depends, not on the quantity of photosensitive substance $S$, but on the concentration of its precursors $P$ and $A$. Because of this, the amount of fresh precursors necessary for a response is always a constant fraction of the amount of precursors already present in the system. The fresh precursors serve to catalyze the simple, chemical conversion of an inactive substance $L$ into one $T$ which then initiates the nervous impulse. This eventually leads to a contraction of the siphon musculature. The reaction system as a whole may be expressed in the following equations:

$$S \rightleftharpoons P + A; \quad L \parallel P + A \parallel \rightarrow T$$

in which $\parallel P + A \parallel$ means catalysis by $P$ or $A$, or both.
The evidence which has already been published has established different phases of this hypothesis. (1) Dark adaptation depends on the regular decrease in the concentration of the residual precursors present in the sensory system. This disappearance of precursors is independent of light, proceeds according to the dynamics of a bimolecular reaction (Hecht, 1918–19, b), and most probably results in the reformation of photosensitive material. (2) This "dark" reaction has a temperature coefficient of 2.4 for 10°C., similar to those usually found for chemical processes. (3) It is quite characteristic of catalyzed reactions that the velocity of the reaction is a linear function of the concentration of catalyst. Similarly we find that the velocity of the second reaction, \( L \rightarrow T \), is a linear function of the concentration of freshly formed precursor catalysts (Hecht, 1918–19, c). (4) The simple chemical nature of the catalyzed reaction, \( L \rightarrow T \), is evidenced by its quantitative behavior in relation to the temperature. It follows the theoretical expectation according to the Arrhenius equation

\[
k_1 = k_0 \left( \frac{1}{T} \right)
\]

in which the velocity constants \( k \) vary with the absolute temperatures \( T \). In this instance the constant \( \mu = 19,680 \), a value characteristic of simple processes like hydrolyses and saponifications (Hecht, 1918–19, d).

In spite of this array of evidence, there is one significant portion of the hypothetical chemical system, the validity of which still remains to be demonstrated. This is the assumption that the reaction \( S \rightarrow P + A \) is really photochemical in nature. In other words, it has still to be proved that the action of the light on the sensory process possesses the ordinarily well demonstrated characteristics of photochemical reactions. The present investigation has therefore been concerned with precisely this aspect of the matter; and it is the object of this paper to show that the initial effect of the stimulus is indeed photochemical in nature.

II.

The experiments were performed with the clam, *Mya arenaria*, which is so common at Woods Hole, Mass. An idea of the appearance of this animal may be obtained from Fig. 1, which is made from
the photograph of a living, medium sized individual expanded in sea water. The extent to which the photosensitive siphon may be protruded is variable; the animal in the figure represents an average condition. On stimulation the siphon is shortened after a clearly defined reaction time. The response is well marked, and involves a movement of the tip of the siphon toward the shell. The amount of this retraction is about 1 cm., often it is more, and it is rarely less than $\frac{1}{2}$ cm. There is never any doubt about the occurrence of a response, nor of the exact moment when the retraction begins. The reaction time may therefore be measured with considerable accuracy.

![Photo of a living bivalve shell](image)

**Fig. 1.** From a photograph of a medium sized, living individual of *Mya arenaria*, expanded in sea water. The reproduction is a little less than life size.

The reaction time is not a simple interval. It consists of two distinct periods. The first is the exposure or sensitization period. This is very short, and is the time occupied by the actually necessary exposure to light. The bulk of the reaction time is composed of the second phase, the latent period. During this period it is not necessary for the siphon to be illuminated. Thus an animal which has been exposed to a flash of light of a few hundredths of a second duration will respond in approximately 2 seconds, even though at that moment it is in the dark.
In order to demonstrate graphically this division of the reaction time, I used an optical recording device. The animal is placed vertically in sand in a glass trough filled with sea water. A fine thread connects its siphon tip with a light heart lever as near the axle as possible. To the opposite side of the axle is attached a small mirror which reflects a beam of light into the slit of the recording camera.

![Image](image_url)

**Fig. 2.** Optical record of stimulation and response, showing the short exposure period and the long latent period. The white streak running the length of the figure represents the movement of a mirror attached to the siphon tip of *Mya.* The white spot and vertical streak at the left record the duration of the exposure (0.07 second). The siphon retracts nearly 2 seconds after the exposure. The slight irregularity in the siphon record immediately following the exposure is due to an accidental vibration of the delicately balanced mirror caused by the movement of the shutter. The tuning-fork marks 0.02 second.

A contraction of the siphon will be shown by an upward movement of the reflected beam. Passing through a shutter is another beam of light. This beam plays on the expanded siphon, and beyond that, directly on the camera slit. On opening the shutter, the beam will

1 Dr. D. J. Edwards was kind enough to let me use his optical recording apparatus, and to give me much of his time and help in the making of records, for all of which I wish to express my gratitude.
therefore stimulate the animal, and at the same time record the exact duration of the exposure on the moving film. The shadow of a vibrating tuning-fork is also focused on the slit, so as to furnish a time record. One of the records obtained in this manner is given in Fig. 2. With an exposure of 0.07 second at this intensity, the retraction of the siphon appears only after a latent period of nearly 2 seconds. A record like that of Fig. 2 is striking testimony of the composition of the reaction time. Since it is our purpose to study the photochemical aspect of photic sensitivity, our attention must therefore be devoted to the relatively short exposure period during which the reception of the light takes place.

III.

Before taking up the nature or the details of the experiments, it is necessary to describe the apparatus which is used for the accurate control of short exposures. In principle the mechanism is that of a focal plane shutter. Its construction may be described with the help of the three views in Fig. 3. Essentially the shutter consists of a piece of black cardboard C, having a variable aperture A which moves with a definite speed past an opening O, through which a beam of light is directed. The duration of the exposure depends on the velocity of the cardboard and the size of the aperture. The rest of the apparatus serves merely to control these two factors accurately and easily.

The variable aperture is obtained by using slides S, each having a different sized opening—all slides, however, having the same weight. A slide is placed in the apparatus by slipping it into the raised grooves G; it is kept in place by them with the help of the raised end-piece P. The front of the shutter may be easily removed for the exchange of slides by turning the thumb screws T. The cardboard C which holds the slide is attached at the bottom to a cylindrical wooden rod R. As it moves across the field the cardboard slides in a simple groove at the top of the shutter, and the wooden rod slides in a metal tube Z.

I made this apparatus by converting a focal plane shutter originally constructed by Mr. J. G. Hubbard. I take this opportunity of thanking Mr. Hubbard for much in the way of advice and material assistance in the building of apparatus used in this work.
at the bottom. When it is at the left of the shutter, the rod is held by a small projecting spring clip F, which may be released by hand, or more conveniently by an air bulb. To the ends of the cylindrical
rod R is attached strong twine, which on the left connects with a
knob K, and to the right leads to the projecting bar M. Therefore
an upward movement of the bar results in the sliding of the cardboard
across the length of the shutter.

The motion of the projecting bar is due to the release of the heavy
brass wire spring NN' wound several times around the screw W.
The tension of the spring and therefore the speed of the shutter may
be varied by placing the arm N' of the spring against the appropriate
raised screw head 1, 2, 3, or 4. The calibration of this movement is
accomplished by recording the excursion of the tip of the bar M on a
rapidly moving kymograph. Several such records gave identical re-
results. A few hundredths of a second after being released, the shutter
slide moves with a constant velocity, which in these experiments is
67.5 cm. per second. The exposure may therefore be computed from
the width of the aperture in the slide, by multiplying the width by
the fraction of a second during which the slide moves 1 cm. ( = 0.0148
second). The front and rear boards of the shutter have raised grooves
V for the insertion of cards having different sized stationary openings
O. In this manner, the dimensions of the beam of light may be
varied. In these experiments the size of the stationary opening is
5 × 35 mm.

To get the shutter ready for use, the opening O is temporarily cov-
ered with a black card, and the knob K is pulled until the shutter
slide C is brought to the left of the shutter. Here it is caught by the
release clip F and held in position. The movement of the shutter
slide C of course pulls the bar M down to the top of the shutter
against the tension of the spring NN'. The temporary card is then
removed, and the shutter is ready for an exposure. At the proper
moment the spring clip is released, and at once the spring NN' exerts
its action. The bar M is jerked rapidly upward and the shutter
slide C is shot past the opening O, thus effecting the proper exposure.

When set up, the shutter as a whole is placed in the front wall of
a light-tight compartment Y (Fig. 4), containing a 250 watt concen-
trated-filament Mazda lamp. The center of the beam through the
opening O is a few millimeters above the level of a long table B. This
is so that the beam will be exactly centered on the siphon of an animal
in a dish of sea water standing on the table. The general arrangement
of the apparatus is shown in Fig. 4. The top of the table B is painted black except for a white streak parallel to the long axis of the light beam. The white streak is a background on which to view the movement of the siphon. In addition the streak is graduated in centimeters marking distances from the center of the source of illumination. In this way the siphon of the animal may be placed at exactly the desired distance from the light, where it will receive the proper exposure from the shutter.

Fig. 4. Arrangement of apparatus in the dark room. The air bulb attached to the spring release clip of the shutter by means of rubber and glass tubings is not shown in the figure. With the help of this bulb and tubing, an exposure can be effected from any position at the work table.

IV.

The first experiments with which I undertook to test the photochemical nature of the light sensitivity were concerned with the relation between the exposure time and the minimum intensity necessary to produce a response. Since the discovery of the Reciprocity Law by Bunsen and Roscoe in 1862, its validity has been demonstrated for a variety of purely photochemical reactions. It obtains whenever the quantity of photic energy necessary to produce a given chemical effect is constant, whether the intensity is low and the exposure long, or the reverse. There are complex reactions, partly photochemical
in nature, which do not obey the reciprocity rule (Schwarzschild, 1899). However, when a process does proceed according to this dictum, it is highly probable that its basis is a simple photochemical reaction.

The usual procedure in investigations of this kind is to vary the intensity and to determine the time required to produce a given effect. This course was adopted with Ciona, and the results bore out the Bunsen-Roscoe expectation (Hecht, 1918–19, a). Such a technique is entirely out of the question with Mya. The exposure required is so short that the errors of measurement would be too great. It is simpler to keep the exposure time under control, and measure the minimum intensity necessary to elicit a response with different exposures. Six exposures were chosen for experimentation. Their durations are given in Table I, first column.

<table>
<thead>
<tr>
<th>Exposure (t.) (sec.)</th>
<th>Intensity (I.) (meter candles)</th>
<th>$I$-4 (meter candle sec.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.016</td>
<td>334</td>
<td>5.34</td>
</tr>
<tr>
<td>0.023</td>
<td>238</td>
<td>5.47</td>
</tr>
<tr>
<td>0.030</td>
<td>194</td>
<td>5.82</td>
</tr>
<tr>
<td>0.053</td>
<td>112</td>
<td>5.94</td>
</tr>
<tr>
<td>0.073</td>
<td>76</td>
<td>5.55</td>
</tr>
<tr>
<td>0.104</td>
<td>54</td>
<td>5.62</td>
</tr>
</tbody>
</table>

Average .......................................................... 5.62

Eight animals which had been thoroughly dark-adapted were used. Taking a given exposure, I subjected each animal in turn to it, and noted whether it responded or not. After each animal had been given a rest of at least 15 minutes, it was again exposed, nearer or farther from the light depending on the individual's previous response. In this way the distance at which a response was elicited was gradually approximated to the distance at which no response could be elicited. I considered a determination as finished when the "no response" distance was 1 cm. farther than the "response" distance. Frequently
the last readings were repeated a few times. An example of an experiment which will indicate the procedure is given in Table II. The entire series of experiments took 6 days, the same animals being used throughout. They were in good condition after the experiments, and remained alive in the laboratory for many days afterwards.

From the determination of the individual minimum distance, it is simple to calculate the minimum intensity by the inverse square law. This was done for each animal for every exposure before an average value was made. A summary of the experiments, giving the average figures, is shown in Table I and graphically in Fig. 5. The third column of Table I shows clearly enough that the Reciprocity Law of Bunsen and Roscoe holds true for this form of photic sensitivity. The curve drawn in Fig. 5 is a theoretical one on the assumption that the photochemical effect \( E \) is a function of the intensity \( I \) and the exposure \( t \), so that

\[
E_k = I \cdot t = 5.62
\]
k being a constant. The deviations of the average experimental points from the theoretical hyperbola of Fig. 5 are not great. In fact the probable error of any individual determination is 6.7 per cent of the mean value assumed in drawing the hyperbola in Fig. 5.

![Graph](image)

**Fig. 5.** Relation between exposure and minimum intensity necessary for a response. The points are the average experimental values. The curve is an hyperbola, \( I_1 = 5.62 \), drawn from the theoretical expectation of the Bunsen-Roscoe law.
On the basis of these results, there seems good reason to believe that the initial action of the light on the sense organ is photochemical in nature. This is precisely what we have assumed in our hypothesis. However, there is still another test possible in this connection, and it was also applied in the study of the effect of the light on the photosensory process.

V.

It is almost axiomatic to say that photochemical reactions possess low temperature coefficients, very near 1.00 for 10°C. (Sheppard, 1914, p. 304). The obvious thing, therefore, is to determine the effect of the temperature on photoreception.

TABLE III.

Minimum Stimulating Distance at Different Temperatures.

Animal 186, August 20, 1919, exposure, 0.016 second.

<table>
<thead>
<tr>
<th>Time</th>
<th>Temperature</th>
<th>Distance</th>
<th>Response</th>
</tr>
</thead>
<tbody>
<tr>
<td>11.05</td>
<td>24.3</td>
<td>57</td>
<td>R.</td>
</tr>
<tr>
<td>11.10</td>
<td>24.5</td>
<td>58</td>
<td>N.R.</td>
</tr>
<tr>
<td>11.15</td>
<td>24.3</td>
<td>57</td>
<td>R.</td>
</tr>
<tr>
<td>11.20</td>
<td>24.9</td>
<td>58</td>
<td>N.R.</td>
</tr>
<tr>
<td>11.25</td>
<td>24.5</td>
<td>57</td>
<td>R.</td>
</tr>
<tr>
<td>11.30</td>
<td>24.1</td>
<td>58</td>
<td>N.R.</td>
</tr>
</tbody>
</table>

R. = Response elicited.
N. R. = No response elicited.

Here again it is of the utmost importance to distinguish between the two periods of the reaction time. The reaction time as a whole possesses a high temperature coefficient. For this, however, the effect of temperature on the latent period is entirely responsible (Hecht, 1918–19, d). Therefore, if our results are to be of the desired significance, we must study the relation between the temperature and the occurrences in the exposure period only. For the same reasons as before, this resolves itself into a determination of the minimum intensity necessary to elicit a response at different temperatures with a given exposure.
The experiments were conducted as previously outlined, except that 5 minutes were allowed between tests. This time has been found sufficient for the complete recovery from a single stimulus. Using a constant exposure of 0.016 second, I determined the minimum intensity necessary to elicit a response at four different temperatures. When the minimum stimulating distance was found, the determination was checked at least twice. Table III gives the details of a portion of one such experiment, wholly typical of the others. Proper precautions were, of course, observed for the maintenance of a fairly constant temperature, etc. In this respect Mya is a particularly good experimental animal, because it helps to stir the sea water by means of its own continuous water current.

![Diagram showing the relation between temperature and minimum intensity necessary for stimulation. The points are single determinations for each experiment shown.](image)
After some preliminary tests, four carefully controlled experiments were made, several days apart. The results were so uniform that further experimentation was deemed unnecessary. The data for the individual experiments are given graphically in Fig. 6. It will be seen that the effect of the temperature of the animal on the minimum stimulating intensity is practically negligible. The temperature coefficients for 10°C. (15–25°), calculated in the ordinary way from Fig. 6, are 1.04, 1.06, 1.07, and 1.06 respectively for Experiments 184, 185, 186, and 187. These values are so characteristic of endoenergetic photochemical reactions, that, combined with the applicability of the Bunsen-Roscoe law, they can lead to but one conclusion. This is that the initial effect of the light in photic stimulation is a purely photochemical phenomenon rather simple in nature.

VI.

As a result of these two sets of experiments we are justified in accepting the proposed hypothesis with a reasonable degree of confidence. Of course the hypothesis is not final. At each step in its construction I have usually suggested an alternative which is less simple than the one eventually adopted. Therefore, it may be necessary to make alterations in the details of the hypothetical chemical system as further evidence accumulates.

One consideration, however, remains of paramount significance and must be the basis of any possible explanation of this kind of photosensitivity. This is that the mechanism of photoreception is not a single process. Corresponding with the division of the reaction time into an exposure or sensitization period and a latent period, there is a fundamental division of the underlying machinery into an initial photochemical reaction and a consequent ordinary chemical reaction. This duality is patent in every experiment with *Ciona* and *Mya*.

Whether the initial photochemical reaction is strictly reversible or only pseudoreversible depends in a large measure on the relation between the primary and secondary reactions of photoreception. It is often as compatible with the data to assume the primary reaction to be
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\[ S \xrightarrow{\text{light}} P + A \]
\[ S \xleftarrow{\text{"dark"}} P + A' \]

in which \( A' \) is an accessory precursor different from \( A \), as it is to assume it to be

\[ S \xrightarrow{\text{light}} P + A \]
\[ S \xleftarrow{\text{"dark"}} P + A. \]

If, as we have postulated, the secondary is catalyzed by the products of photolysis of the primary reaction, then the primary reaction is to be considered as strictly reversible. If, however, the reaction between the two is conceived to be in the nature of a catenary chemical interaction, then a pseudoreversible reaction is a more likely possibility for the primary process than a strictly reversible one. Even in this instance, a photochemical reaction is feasible, if the secondary process itself is assumed to be reversible.

None of these alternatives, however, appear very attractive because of their innate complexity. This becomes especially true when it is necessary to make a mathematical analysis of data in order to compare theoretical expectation and actual performance. The proposed hypothesis of photoreception is therefore to be preferred in its present form, unless some glaring discrepancy arises.

VII.

Aside from their significance with regard to an hypothesis of photoreception, these experiments involve some general conceptions of rather wide application. In the study of the responses of organisms much agitation has resulted over the difference between those individuals which are sensitive to the continuous action of light, and those which are sensitive to a rapid change in the intensity of the light only. The distinction as it is usually made rests on the assumption that for the one group the effective stimulus is a definite quantity of light, whereas for the other group the effective stimulus is the rate of change of the intensity. The conception underlying this differentiation, however, is as fallacious as it has been common. I have no desire to enter into a controversy which has been continued much too long. But the
experiments on *Ciona* (Hecht, 1918-19, a) and *Mya* have demonstrated that the distinction on which this controversy rests is without any but the most superficial basis.

The facts are simple enough. Blaauw (1909) and Fröschel (1909) demonstrated that the orientation of certain plants obeys the Reciprocitv Law of Bunsen and Roscoe; therefore a definite amount of light is required for a stimulus. Loeb (1918) and his associates proved the same to be true for the animals with which they experimented. All these organisms are, of course, to be classed in the group which responds to an obviously continuous source of illumination.

On the other hand, *Mya* and *Ciona* belong decidedly in the group of organisms which is sensitive to light only when the illumination intensity has been increased rapidly. And yet both *Mya* and *Ciona* must receive a definite amount of light before they respond. In *Ciona* this is approximately 5,000 meter candle seconds; and in *Mya*, as we found in this paper, the required energy is about 5 meter candle seconds. The stimulus for both groups of organisms is therefore the same, a definite quantity of light energy producing a specific photchemical effect. Certainly no distinction can be made between them on this score.

One point remains to be elucidated. Since both groups of organisms require fundamentally the same stimulus, how is it that animals like *Mya* and *Ciona* respond apparently to sudden illumination only? This is indeed a paradoxical situation, yet the answer to the question is simple. The explanation depends on the reversible character of the sensory process.

The presence of a regenerative mechanism in the sense organ is shown by the course of dark adaptation. The photosensitive material decomposed by the light is automatically regenerated as soon as some products of decomposition accumulate. The velocity of this regenerating reaction depends on the concentration of the precursor decomposition products. Therefore a little time must elapse before the effect of the regenerating reaction will become apparent. It is precisely during this short interval of time that the required amount of energy must be received by the sense organs in order to produce a response.
Physically speaking, this energy requirement means that a definite mass of sensitive substance is decomposed by the light. When the energy is delivered rapidly, that is when a high illumination is attained suddenly, the necessary photosensitive substance is decomposed before the regeneration reaction sets in. But if the energy is delivered slowly, sufficient sensitive substance to produce a response cannot be decomposed before the "dark," regeneration reaction becomes effective. The "dark" reaction, once under way, proceeds slowly or rapidly depending on the rate at which the light decomposes the sensitive substance into its precursors. As a result, a stationary state is attained analogous to a condition of true equilibrium, in which no amount of exposure to light can form enough precursors to initiate a response. Even if the intensity continues to increase to a very high value, no effect can be produced as long as the increase is slow, simply because a new stationary state of the opposing reactions will be reached if enough time is allowed.

The time interval during which the necessary amount of energy must be delivered is known experimentally. In *Ciona* the 5,000 units of energy must be received within about 10 seconds; in *Mya* the required five units must enter the sense organ in less than 1 second. The time limit is thus greater in *Ciona* than in *Mya*. This time interval, as we have said, depends on the speed with which the regeneration reaction proceeds. Therefore the regeneration reaction in *Ciona* should be slower than in *Mya*. This is indeed the situation. Dark adaptation is wholly dependent on the regeneration reaction (Hecht, 1918–19, a, b). In *Ciona*, dark adaptation requires about 4 hours, whereas in *Mya* the same process is complete in about 35 minutes. The time limit for the energy delivery is thus proportional to the velocity of the "dark" reaction which regenerates the sensitive substance.

The conclusion is clear. In spite of the apparent sensitivity of animals like *Mya* and *Ciona* to sudden illumination the effective agent for this sensitivity is a definite quantity of energy which obeys the Reciprocity Law of photochemistry. The fact that this amount of light energy must be received by the sense organs in a limited time is merely a concomitant of the additional circumstance that the photochemical reaction is reversible. The rate of change of the light inten-
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sity is decidedly not the effective stimulus. Therefore the contro-
versial division of organisms into the two groups previously mentioned,
though traditionally sacred, is fundamentally without significance.
The effective stimulus in photic irritability is of the same nature
whether the response is to a light which is obviously continuous, or
to a light whose intensity is suddenly augmented.

SUMMARY.

1. In order to produce a response in *Mya*, the minimum amount of
light energy required is 5.62 meter candle seconds. This energy fol-
lows the Bunsen-Roscoe law for the relation between intensity and
time of exposure.

2. The necessary minimum amount of energy varies but little with
the temperature; the temperature coefficient for 10°C. is 1.06.

3. In view of these facts it is concluded that the initial action of the
light is photochemical in nature. This substantiates the hypothesis
previously suggested to account for the mechanism of photoreception.

4. The constant energy requirement for stimulation of *Mya* shows
that the traditional division of animals into those which respond to a
constant source of light and those which respond to a rapidly aug-
mented light is without any fundamental significance for sensory
physiology.

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